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What defines an edge? Quantifying edge effects across multiple trophic levels

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What defines an edge? Quantifying edge effects across multiple trophic levels

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Dedication

This work is dedicated to the people who have supported me and cheered me on as I reached for the stars. To the mentors and teachers who saw potential and worked to nurture it. To the people I am lucky enough to call my friends who have always had my back, and finally to my family who loved and support me unconditionally every step of the way.

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Abstract

What defines an edge? Quantifying edge effects across multiple trophic levels

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Habitat fragmentation is often cited as a primary driver of biodiversity loss across biomes. Spatial habitat fragmentation causes an increase in edge habitat relative to interior which may provide different value as they often vary in functionality. There is a general lack of consensus regarding the distance that delineates edge versus interior limiting the ability to accurately capture edge effects on seagrass ecological function. As fragmentation is accelerating, it is necessary to understand the factors driving edge effects to better predict the effect of changes in habitat configuration. My work measured community metrics in seagrass ecosystems at varying distances from the edge to understand edge effects driving organismal response to habitat fragmentation. First, I sampled seagrass beds in 2018 for a post-disturbance study one year after Hurricane Harvey hit Texas. I sampled along seagrass patch edges and interior to quantify seagrass morphometrics and biomass, benthic macrofauna and nekton communities. Next, I conducted a fine-scale study in 2019 sampling seagrass beds along 10 meter transects

from the edge in towards bed interiors in the same region to quantify nekton and macrofaunal communities, seagrass metrics, predation risk, and flow at a precise scale. Across both studies, I found increased seagrass biomass in habitat interiors that was most pronounced around 2 meters in one study. I saw higher temperature and epiphyte biomass with increased distance from seagrass edge in the fine-scale study and across studies there were no demonstrated edge effects on benthic macrofaunal community composition, predation risk or flow. There was a positive effect on nekton diversity in the post-disturbance study driven by matrix spillover of species associated with soft muddy bottoms. Results suggest pronounced edge effect for seagrass itself, and ecologically defined edges may be larger than the edge sizes assumed in many past studies highlighting the need for edge designations to be scaled to the response variables tested in order to accurately capture edge effects. Multi-trophic and continued empirical measurement of habitat edges may help resolve differential responses across studies and predict the effects of anthropogenic habitat fragmentation on the ecological function of critical nearshore habitat like seagrass.

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Introduction

Habitat fragmentation is often cited as a primary driver of biodiversity loss across biomes (Rand et al. 2006). Habitat fragmentation of marine ecosystems may be caused by both natural and human disturbances like extreme storm events (Fourqurean and Rutten, 2004), coastal development (Peterson and Lowe, 2009), physical damage from boat propellers (Uhrin and Holmquist, 2003), or nutrient loading (Short and Burdick, 1996). As many of these anthropogenic and natural drivers of fragmentation are accelerating, understanding how changes in habitat configuration impact ecological function is increasingly important. Habitat fragmentation involves a loss in total habitat area along with a breaking apart of remnant habitat (Hovel 2003). One consequence of the spatial fragmentation of habitat is an increase in edge habitat relative to interior habitat ratios. Past studies have found that habitat edges may function differently than habitat interiors (Davies-Colley et al. 2000) and thus edge effects have been often cited as a major driver of impacts of fragmentation on community composition (Smith et al. 2008).

Edge habitat is defined as the transition between habitats with different structural complexity (Carroll and Peterson, 2013). Habitat edges may provide different habitat value than interiors as they may vary in habitat structure, predator-prey interactions, or environmental conditions (Murphy et al. 2010). Organismal responses to habitat edges may be species-specific, however. Specifically, one study found polychaetes and molluscs occurred in higher abundance along salt marsh habitat edges than habitat interiors (Whaley and Minello 2002), indicating a positive effect of edge. In contrast,

other studies show negative responses to edge habitat, such as decreased abundance along mangrove forest edges relative to interiors in snails *Neritina virginia* (Amortegui-Torres et al. 2013). Thus, edge effects do not appear to be uniform across habitats and species. Understanding the factors driving edge effects is therefore necessary to better predict the effect of changes in habitat configuration on ecological structure and function.

In marine systems, water flow may be a primary factor mediating edge effects. Water flow dictates larval supply and delivery of nutrients and particulates across habitat boundaries. Within structured environments like seagrass beds or reef systems, the physical structure of the habitat can serve to reduce water velocities and promote particle settlement (Peterson et al. 2004, Hendriks et al. 2008). In particular, edges of seagrass habitat have been shown to experience more dynamic flow conditions and increased scouring and canopy movement (Fonseca et al. 1982, Ackerman and Okubo 1993). This increased canopy movement along with reduced numbers of surrounding shoots can reduce self-shading and promote productivity along bed edges. Higher water flow along habitat edges may also convey more larvae to edge habitat, translating to increased settlement of larval-dispersing species. For example, seagrass beds that were near high-volume channels had a greater abundance of larvae relative to those in lower flow environments (Ford et al. 2010). For water-column or filter feeding consumers, increased water flow may also increase the food supply. Macreadie et al. (2009) found pipefishes (*Stigmatopora argus, Stigmatopora nigra*) had no change in abundance across a gradient of increased habitat fragmentation and suggested that higher encounter rates of planktonic crustaceans along seagrass edges counteracted loss in foraging area due to loss

in total habitat. Likewise, filter-feeding bay scallops (*Argopecten irradians*) experienced higher settlement and growth rates along seagrass edges relative to seagrass interiors due to increased water flow and delivery of food (Irlandi et al. 1995).

By definition, habitat edges encompass adjacent habitats with differing structural complexity. The higher habitat heterogeneity along the habitat edge may therefore increase niche diversity with cascading impacts on biodiversity (Darimont et al. 2009). Furthermore, edges of habitats may exhibit differences in structural complexity (e.g., plant density) from habitat interiors. Bologna and Heck (2002) found increased density in turtle grass (*Thalassia testudinum*) within bed interiors compared to habitat edges. As structural complexity is key in providing refuge for smaller and less mobile organisms (Warfe and Barmuta 2004), differential structural complexity along habitat edges may alter predator-prey interactions. For example, Bologna and Heck (1999) found lower bay scallop (*Argopecten irradians*) survival along seagrass edges which may have been driven by lower shoot densities. Conversely, Mahoney et al. (2018) found increased survivorship along the edge for tethered blue crab (*Callinectes sapidus*) and pinfish (*Lagodon rhomboides*) relative to interior. The impact of edges on organismal response should therefore depend on whether edges display increased or decreased structural complexity. Likewise, accessibility of matrix habitat is another potentially important driver of edge effects. Species within matrix habitats have easiest access to the edges of the adjacent habitat types, and thus matrix predators may spillover and feed along edges of adjacent habitat. Furthermore, some predators may preferentially target habitat edges for feeding as edges have high prey concentrations and can be ideal foraging habitats

(Smith et al. 2011; Macreadie et al. 2010). For example, juvenile southern flounder and red drum were shown to preferentially utilize edge seagrass habitat as foraging grounds (Dance and Rooker, 2015).

While edge effects have been extensively studied in marine systems, there is no clear consensus on how edges are defined, thus limiting the ability to synthesize edge effects across systems (Carroll et al. 2019). Typically, an arbitrary fixed distance from the habitat boundary is selected by the investigator and applied across study sites. The fixed distance chosen has varied among studies with different habitat patch sizes and study organisms without a standardized ecological framework to delineate habitat edges. In a recent review, Carroll et al. (2019) compiled edge sizes across 71 studies from marine ecosystems and noted that edges as defined by study authors ranged from 0.03-20 m in width, with the vast majority using a distance within 5 m to represent the edge. Inconsistent or inappropriate edge definitions may lead to erroneous inference about the importance of edge effects and may in part explain the wide variation in the nature and magnitude of edge effects across studies and ecological responses considered.

Furthermore, how species perceive and respond to edge effects likely varies based on their traits. For example, trophic level may be expected to play a role in determining edge habitat trade-offs. Mahoney et al. (2018) found higher survival for mesopredators blue crab (*Callinectes sapidus*) and pinfish (*Lagodon rhomboides*) along the edges in contrast to past studies focused on primary consumers documenting lower survival along edges (e.g., Bologna and Heck 1999, Carroll et al. 2013). Similarly, body size may be important in determining edge effects as size will mediate organismal interactions with

refugia and the scale at which organisms respond to environmental heterogeneity (Jackson and Fahrig, 2015). Yeager et al. (2019) found that smaller-bodied species were more sensitive to microhabitat variation associated with habitat fragmentation while larger-bodied species responded more strongly to landscape-scale variation. Thus, studies investigating edge effects measured at a single fixed distance may fail to capture responses across multiple taxa. More multi-scaled and trait-based approaches should help to resolve when and where edge effects occur, ultimately better informing models of how habitat fragmentation drives ecosystem function in marine systems.

OBJECTIVES AND HYPOTHESES

I chose to use seagrass ecosystems as a model to better understand how edge effects drive organismal responses to fragmentation**.** First, I investigated edge effects in seagrass beds following Hurricane Harvey comparing abundance and diversity of multiple trophic levels between seagrass interiors and edges in order to take advantage of the natural disturbance and associated habitat fragmentation that occurred. Second, I conducted transect surveys in order to examine fine-scale (20 cm) spatial patterns at varying distances (0-10 m) from habitat edges in a variety of ecological variables. My goal was to quantify edge effects across ecological response variables, species, and trophic levels. As organisms have variable requirements for oxygen, nutrients, and habitat dependent on their traits, I predicted that they would respond to habitat edges at different spatial scales. Specifically, I hypothesized that:

H1: Water flow will be higher at the edge of the seagrass bed versus the interior, but this effect will attenuate quickly. Salinity and temperature will show minimal variation across the edge to interior axis.

H2: Lower trophic level species that may be more sensitive to flow and small-scale shifts in environmental conditions (e.g., seagrass, filter feeders) will respond to habitat edge at smaller scales.

H3: Larger bodied, mobile predators will respond to habitat edges at larger scales or demonstrate no edge effects as they should respond to habitat variation at coarser scales.

H4: Predation risk will be highest along seagrass edges for benthic macrofauna and juvenile fish and be primarily mediated by difference in structural complexity as opposed to consumer presence and will therefore respond to edge effects at smaller spatial scales.

Methods

STUDY SITES

Post-disturbance edge study

Hurricane Harvey struck the Texas coast in August, 2017 causing widespread, patchy loss of seagrass, specifically in *Thalassia testudinum* beds (Congdon et al. 2019). Damage from the storm was concentrated within the region of Redfish Bay with scouring and sediment deposition resulting in the loss of seagrass patches ranging from meters to 100's of meters. Seagrass beds in this region are dominated by *Thalassia testudinum,* a slow-growing, climax seagrass species with a wide distribution from the Gulf of Mexico through the greater Caribbean Sea (Peterson et al. 2002). As seagrass productivity peaks in the summer months in Texas, we conducted targeted edge effect sampling following the storm during the summer of 2018 (Fig. 1).

Fine-scale edge study

Following the disturbance study, I planned a finer -scale study to evaluate spatial scales of edge effects within the same region of the Texas coast. I conducted field surveys to explore high-resolution patterns in ecological variables at varying distances from habitat edge within four *Thalassia testudinum* dominated seagrass beds (Fig. 2). I sampled the seagrass beds in the summer of 2019 and each bed was characterized by a contiguous area of seagrass at least 20 m long and 15 m wide. All four focal seagrass beds were bordered by unvegetated bottom and had a range of depths from 75-145 cm.

DATA COLLECTION

Post-disturbance edge study

Seagrass cores were collected at 16 beds resulting in one edge and interior core for each site. Edge was designated as the seagrass directly along the sand interface and interior as a spot at least 2 meters into the bed from the edge. Cores were taken using a 9-cm diameter PVC hand core which sampled to a depth of 17 cm. After sampling, each core was bagged in a resealable plastic bag, transported to the laboratory on ice, and frozen at -3°C until processing. In the laboratory, each core was sieved with a 1 mm mesh size sieve and above and below ground biomass was separated. All shoots were counted, and up to 5 representative shoots were chosen and blade height and blade width measured before being scraped of epiphytes. The epiphytes were transferred to pre-weighed glass fiber filters. Filters, representative seagrass blades, total aboveground and total belowground biomass were dried in a 60°C oven for one week and then weighed on an analytical balance to obtain dry weight. All fauna were separated from any remaining sediment and shell hash. Fauna were counted, identified to genus or species, and up to 10 representative individuals per taxa were blotted dry and then weighed to estimate biomass (wet weight).

To quantify the nekton community, I used baited minnow traps at eight sites. On each sampling date, four traps were set at each site: two traps designated as the edge trap that were set directly on the seagrass to sand interface and two interior traps that were set at least 2 meters from the edge. All seagrass patches sampled were at least 4 meters across or larger. The traps were baited with dog food and left out for 24 h sets. This was

done twice; once in July and once in August for a total of 61 traps. Upon collection, all species were identified, measured, and released.

Fine-scale edge study

At each of the four study sites, I conducted fine-scale surveys to measure spatial patterns in a suite of abiotic and biotic parameters (Table 1). Specifically, I sampled along replicate 10m transects in each seagrass bed from the edge to interior. I selected sampling sites within seagrass beds that were large enough to ensure a 10 m transect did not cross the middle of the bed to eliminate/minimize edge effects on the interior end of the transect. Edge was defined as the transition from completely unvegetated bottom to seagrass structure and was set as the 0 cm distance along the transect. Samples were taken at set distances from the edge towards the interior of the bed (sample distances varied across variables, see below).

To evaluate seagrass structural complexity, benthic macrofauna community structure, and environmental parameters, samples were collected at 16 points along the 10 m transect at 0, 20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 250, 300, 500, 700, and 1000 cm. I collected one benthic core at each distance to estimate measures of seagrass structure (above and belowground biomass, shoot densities) as well as benthic macrofauna composition and density. These cores were processed with the same methodology as the aforementioned cores from the post disturbance study. I recorded salinity, temperature and conductivity with a YSI 600 XLM sonde at each sampling point and these measurements were taken within 30 minutes of noon. In order to document diel

patterns in conductivity and temperature, I measured at 4 distances from the seagrass edge: 0, 50, 200, and 500 cm. HOBO U24 conductivity data loggers were placed within half cinder blocks and set for 48 h at each distance and recorded salinity and temperature every one min. The collection time started twenty minutes after deploying the loggers and the next 48 hours were compared across the sites. The mean temperature and salinity were calculated from the 2880 time points and range was determined by subtracting the lowest point from the highest point at each site.

Nekton community composition and predation rates were assessed at 10 transect distances: 0, 40, 80, 120, 160, 200, 300, 500, 700, and 1000 cm. To ensure independence across distance measurements for more mobile taxa within a site, measurements were staggered along five separate transects set out from the edge of the bed with at least 3 m between each transect and 1 m between any distance replicate. As a metric of relative predation risk, I set out tethering assays using squid pops (Duffy et al. 2015a). Squid pops are 1 cm circles of dried squid attached to stakes that are driven into sediment and left for a set time. I set ten squid pops at a time out for 1 h and then recorded the presence or absence of the squid. To quantify the nekton community, I used baited minnow traps. The traps were baited with dog food and left out for 4 h sets. Upon collection, all species were identified, measured and released. Any species that could not be identified in the field were euthanized with an overdose of eugenol and seawater mixture and then put on ice for transport to the lab for final identification.

In order to measure water flow, plaster cubes were deployed at 10 transect distances: 0, 40, 80, 120, 160, 200, 300, 500, 700, and 1000 cm. Plaster cubes were put

out in 72 h sets as pilot trials determined this amount of time allowed for measurable plaster loss. The plaster cubes (clod cards) are used to measure a proxy of flow by equating increased plaster erosion with increased water flow (Thompson and Glenn 1994). I mixed 1-part plaster of paris with 1-part water and dried them for 72 hours in the lab modeled after the methods in (Doty 1971). Each cube was weighed and sanded down to within 0.01g of the goal weight for consistency across all cubes. After sanding, cubes were glued to plastic sheeting and weighed for a final starting weight. Each plastic cube combo was attached to a 9-cm by 9-cm tile and secured in the seagrass bed with garden stakes. Upon retrieval, the cubes were air dried for 48 hours and weighed and the total loss calculated.

Due to COVID-19, I halted sample processing of seagrass and sediments cores as well as remaining fieldwork in March 2020. Data in this document is from up to that month resulting in the loss of data from the remaining cores. Included in the missing samples are 26 out of 64 total seagrass cores. This resulted in two complete transects (CC1 and CC3) processed out of a total of four sampled transects for seagrass variables and benthic macrofauna measurements, and two transects (CC1 and CC2) for water flow. All remaining variables were quantified along all four transects.

DATA ANALYSIS

Post-disturbance edge study

I compared a suite of ecological response variables between interior and edge samples in the post-disturbance studies including measurements of nekton community composition,

benthic macrofaunal composition, epiphyte biomass, seagrass biomass, and seagrass shoot density. For the nekton and benthic macrofauna data, I calculated community metrics as follows: abundance was the total number of organisms in an individual core or minnow trap, species richness was the count of different species in a core or trap, and species evenness was Shannon's diversity index H divided by the natural logarithm of species richness. I ran linear regression models to compare each ecological response variable with bed position (edge vs. interior) treated as a fixed effect. Site was included as an additional fixed effect to account for non-independence of edge and interior samples taken from the same site. I used the lm function in R to analyze the linear regression models and I used the Anova function in the car package (Fox and Weisberg 2019) with type II sums of squares to evaluate the statistical significance of fixed effects (R Core Team, 2020). As an additional measure of effect size, I used the lsr package (Navarro 2015) to calculate $\eta 2$ which estimates the independent variation in the dependent variables predicted by each independent variable in the model. In order to compare differences in community structure for benthic macrofauna and nekton communities, I ran a Permutational Analysis of Variance (PERMANOVA; Anderson 2001) on square-root transformed species abundance by sample matrix using the adonis function from the vegan package (Okansen et al, 2019) in R with bed position (edge vs. interior) treated as a fixed effect. Then, I used simper in the vegan package to determine individual species driving any observed patterns by finding the average contributions of each species to the overall dissimilarity matrix. Finally, as fine-scale seagrass structure is expected to influence benthic macrofaunal community, I ran pairwise Pearson

correlations between seagrass biomass and seagrass shoot density and benthic macrofaunal abundance and species richness.

Fine-scale edge study

For the nekton and benthic macrofaunal data, I calculated community metrics as in the first study: abundance was the total number of organisms in an individual core or minnow trap, species richness was the count of different species in a core or trap. Next, I ran linear regression models to compare each ecological response variable with distance (cm) from the edge. Site was included as an additional fixed effect to account for non-independence of multiple transect measurements taken from the same site. As above, I used the lm function in R to analyze the linear regression models and I used the Anova function in the car package with type II sums of squares to evaluate the statistical significance of fixed effects and calculated η^2 as an additional effect size measure (R Core Team, 2020). Because many of the benthic macrofauna and nekton samples returned few or zero individuals in this study, I focused my analysis on total faunal abundance and taxa richness rather than including evenness and community structure based on Bray-Curtis dissimilarity metrics as in the post-disturbance study. As above, I ran pairwise Pearson correlations between seagrass biomass and seagrass shoot density and benthic macrofaunal abundance and species richness across cores to determine whether fine-scale seagrass structure may have driven differences in benthic macrofauna community metrics.

Results

POST-DISTURBANCE EDGE STUDY

Seagrass Data

The effect of edge position varied across primary producer response variables. Seagrass biomass showed a negative response to habitat edges, with 34% less total seagrass biomass on average being found within cores along seagrass edges than those placed within seagrass interior (Fig. 3, Table 2). This trend was driven primarily by below ground seagrass biomass, with 51% less belowground biomass along seagrass edges than interiors; while mean aboveground seagrass biomass showed a similar trend, there was no consistent difference between edge and interior cores (Tables 3-4). In contrast to seagrass biomass, seagrass shoot density and epiphytic biomass did not vary with position within seagrass beds (edge vs. interior locations) (Figs. 4-5, Tables 5-6). Seagrass shoot density and epiphyte biomass were found to be highly variable among sites, however, with the site effect explaining 46% and 68% of the variation in the response variables, respectively (Tables 5-6).

Benthic Macrofauna Data

Benthic macrofaunal community composition was unaffected by edge or interior bed position. Benthic macrofaunal abundance, species richness, and evenness were all similar between seagrass edges and interiors, although there was high variation among sites for all response variables (Figs. 6-8, Tables 7-9). Site explained a large amount of variation across the response variables ranging from 43-73%, while position explained a

maximum of 3% of the variation in benthic macrofaunal community response variables (Tables 7-9). Exploring the relationship between benthic macrofaunal response variables and seagrass structure showed a positive relationship between seagrass biomass and benthic macrofaunal abundance (P-value: 0.001, r: 0.56), but no strong correlations with benthic macrofaunal species richness or between macrofaunal abundance and seagrass biomass or shoot density (P>0.05, r <.25 In all cases). Likewise, benthic macrofaunal community composition was similar between edge and interior cores (Fig. 9) (PERMANOVA, position: P-value=0.25, R^2=0.03).

Nekton Data

In contrast to the benthic macrofaunal community data, nekton community composition differed between seagrass edges and interiors with generally small site effects. There was no difference between edge and interior or among sites for both nekton abundance and nekton species evenness (Fig. 10-11, Tables 10-11). However, edge habitats had higher nekton species richness than interior (Fig. 12, Table 12) and similarly there was a shift in overall community composition of nekton in minnow traps between seagrass edges and interiors as determined by a PERMANOVA (Fig. 13) (Position: P-value=0.03, R^2=0.07) and visualized with an MDS plot. The species driving this compositional difference were identified as *Eucinostomus argenteus* (P-value=0.003), *Lutjanus griseus* (P-value=0.004), *Callinectes sapidus* (P-value=0.008), and *Gobiosoma bosc* (P-value=0.04) which were either more abundant or only found in traps along habitat edge.

FINE-SCALE EDGE STUDY

Environmental Data

Patterns in environmental variation with distance from habitat edge varied among response variables considered. From point measurements, there was a weak effect of distance from the edge on temperature, which increased and average of 0.6°C every m as distance from the edge increased (Fig. 14, Table 13). Unlike temperature, there was not an effect of distance from the edge on salinity and small site effects (Fig. 15, Table 14). Data logger temperature over 48 hours at 0, 50, 100, 200, 500 centimeters from the seagrass edge showed no effect of distance on mean or range with site explaining 95% and 91% of the variation in each variable, respectively (Fig. 16, Tables 15-16). Similarly, data logger salinity over 48 hours at 0, 50, 100, 200, 500 centimeters from the seagrass edge showed no effect of distance from edge on mean or range, however site had some effect upon salinity at 60% and 30% explained respectively (Fig. 17, Tables 17-18). Similarly, plaster loss did not show a relationship with distance from the edge, however there were large differences among the two sites (Fig 18, Table 19).

Seagrass Data

Primary producers displayed negative edge effects across the two transects measured for all three response variables: seagrass biomass, shoot density, and epiphytic biomass. Seagrass total, aboveground, and belowground biomass all displayed an increasing asymptotic pattern with distance from seagrass edge (Fig. 19, Tables 20-22). In contrast with the post-disturbance study, epiphyte biomass (Fig. 20, Table 23) and total

number of seagrass shoots also showed an edge effect and increased with distance from the edge (Fig. 21, Table 24).

Benthic Macrofauna Data

As in the post-disturbance study, benthic macrofaunal community composition (abundance and species richness) was unaffected by distance to the edge (Fig. 22-23, Table 25-26). In this study, the benthic macrofaunal response variables were not related to seagrass structure as there were no correlations between benthic macrofaunal species richness or benthic macrofaunal abundance with seagrass biomass or shoot density ($P > 0.05$, $r < 0.27$ in all cases). Nekton community abundance and species richness also demonstrated no edge response in the fine-scale study, in contrast to results of the post-disturbance study (Figs. 24-25, Tables 27-28). Predation rates varied widely across sites corresponding with site explaining 57% of the variation in predation with no effect of distance from edge (as it explained less than 1% of the variation in predation risk; Fig. 26, Table 29).

Discussion

Bringing together data from post-disturbance habitat sampling and fine-scale field surveys, I found that edge effects within seagrass systems were generally weak and dependent on the response considered. The most consistent edge effect across the two studies was a negative effect of edge on seagrass biomass. It was not clear whether environmental variation may have driven this edge effect on seagrass, as environmental parameters (besides in situ temperature measurements in the fine-scale study) showed no response to edge effects in the fine-scale study, although sample sizes were limited. Furthermore, edge effects on seagrass did not appear to scale up to fauna as faunal responses (e.g., relative predation rates, benthic macrofaunal abundance, and benthic macrofaunal diversity) were found to be highly variable across seagrass sites while within site patterns relative to distance from edge were inconsistent. The exception to the general lack of edge effects in fauna was higher nekton diversity along seagrass edges and differences in community composition found in the post-disturbance study (but not the fine-scale edge study) which may have been driven by habitat spillover from surrounding matrix habitats. Overall, the edge effects were varied and potentially mediated through a wide variety of factors within and among seagrass beds.

The clear edge effect on seagrass biomass is consistent with past literature showing increased seagrass biomass away from habitat edges (Hovel and Fonseca 2005, Bologna and Heck 2002, Marba and Duarte 1995, Moore and Hovel 2010). The negative edge effect was most pronounced for below ground seagrass biomass in both studies, while above ground components showed similar but weaker patterns. Below ground

biomass may be slower to respond to environmental change as roots and rhizomes that take time to develop and store nutrients while shoot density and aboveground biomass only takes into account aboveground growth (Di Carlo and Kenworthy 2008, Mateo et al. 1997). Thus disturbances along edges may have long-lasting impacts on below ground biomass. In the post-disturbance study, specifically, above ground seagrass components may be showing signs of recovering along scoured edges faster than those of the belowground biomass. Similarly, Di Carlo and Kenworthy (2008) found a trend of faster aboveground biomass recovery than belowground after physical disturbance in subtropical seagrasses. Across both studies, proximity to seagrass edges appeared to be altering the structure of the habitat-forming species which should scale-up to lower habitat complexity and potentially productivity along seagrass edges.

Although not consistent between the two current studies, epiphyte biomass also increased towards bed interiors in the fine-scale study. Epiphyte abundance and distribution is a result of many biotic and abiotic factors which can be, but are not always, influenced by edge effects. For example, reduced wave energy in denser seagrass interiors could also lead to reduced scouring and allow higher settlement rates for epiphytic propagules (Vanderklift and Lavery 2000). Additionally, grazing is important in controlling epiphytic abundance and community composition (Prado et al. 2007, Duffy et al. 2015b). While herbivory was not measured in this study, if herbivore abundance or activity varied with bed position, it may have led to variation in relative epiphyte biomass (Hays 2005, Borowitza et al. 2006). Past studies have generally failed to show a clear edge effect on seagrass epiphytes, however. For instance, Sweatmen and colleagues

(2017) found after simulated propeller scarring within seagrass habitat in The Bahamas, that fragmentation did not impact epiphyte biomass (Sweatman et al. 2017). Similarly, Saunders and colleagues (2003) found no effect of distance from the edge on seagrass epiphytic abundance when measured from 0 to 6 meters interior, however the authors acknowledge low power of the distance analysis. Further, they found epiphytic abundance and composition varied considerably amongst-beds rather than within-beds (Saunders et al. 2003); similar to high among-site variability reported herein. Given the limited sample size in the fine-scale study, lack of effect on relative epiphyte biomass in the post-disturbance study, and results of previous studies, there is still little evidence for a consistent edge effect on epiphyte biomass in seagrass systems when compared to that for the seagrass structure itself.

The other notable edge effect found within the current study was a positive effect of nekton diversity in the post-disturbance study. This higher nekton diversity may have been driven by the shift in habitat structure or matrix spillover, i.e., species associated with the adjacent matrix habitat utilizing the seagrass edges (Tanner 2006). Matrix spillover as a primary mechanism driving higher species richness and shifts in species composition along seagrass edges was supported by a higher occurrence of species that are typically associated with soft muddy bottoms such as the Blackcheek Tonguefish (*Symphurus plagiusa*), Naked Goby (*Gobiosoma bosc*), and Spotfin Mojarra (*Eucinostomus argenteus*) along edges (Miller et al. 2015, Walsh et al. 1999, Chen et al. 2007). Furthermore, these animals may be preferentially using the edge of the adjacent seagrass habitat to locate prey in line with past studies showing targeted predation along

edges (Smith et al. 2011). It is possible that similar mechanisms may have been important in altering nekton diversity in the fine-scale study, but were undetected due to more limited sample sizes relative to the post-disturbance study. When considering the impacts of habitat fragmentation on higher-order taxa it is important to include the possibility of positive edge effects driven by species spillover and design studies that can accurately capture these effects.

Contrary to the original hypothesis, benthic macrofauna and relative predation levels showed a lack of response to edge position. Thus, edge effects on seagrass did not appear to scale-up to associated-benthic macrofaunal communities. It is possible that high among-site variability in macrofaunal communities obscured edge effects, or that species-specific trends were not detected in community-level analyses. Some studies have shown increased predation risk along seagrass edges for bivalves and epifauna due to improved visibility and lowered ability to camouflage (Bologna and Heck 2002). This study, however, agrees with the recent findings of Yarnell and Fodrie (2020), showing no demonstrated edge effects on relative predation in temperate seagrass beds. Even as seagrass biomass increased away from edges, this increased habitat structure did not appear to be driving a difference in relative predation. Lack of response in predation risk to seagrass edges aligns with studies observing that predators like fish and mobile epifauna may be robust to extreme changes in seagrass cover (Reed and Hovel 2006, Pittman et al. 2004) or are responding to habitat structure at much larger spatial scales (Yeager et al. 2019). Thus, benthic macrofaunal abundance and relative predation levels

are likely affected by many factors beyond distance from the edge interface, resulting in a lack of consistent response to bed position.

While I did not find clear edge effects on environmental parameters in this study, limited spatial and temporal sampling likely prevented the detection of these effects. Past work has shown that seagrass structure modified key environmental factors, such as water flow. Furthermore, the weak positive relationship between temperature and distance from the edge in the point measurements taken in the fine-scale study suggests that seagrass bed structure could alter environmental conditions in this system. Tide-dominated seagrass beds have unidirectional flows that deflect water over the meadows leading to decreased mixing from water flow towards bed interiors (Bologna and Heck 2002, Fonseca et al. 1982). The weak trend of higher temperature towards the interior of the seagrass bed was possibly caused by decreased water flow from increased shoot density (Koch and Gust, 1999). Future studies on fine-scale edge effects could benefit from coupled fine-scale flow measurements to better determine possible effects upon seagrass beds.

Although the results of the fine-scale study were limited in terms of sample size, these preliminary findings did support the importance of chosen edge size in determining the nature of edge effects. Specifically, my results provide support for seagrass edge designations slightly larger than two meters as there was a visual increase in seagrass total biomass and seagrass shoot density between two to three meters from the edge in the fine-scale study. This 2-m edge is larger than the 1-m size used in many previous studies of seagrass edge effects (Carroll et al. 2019), suggesting larger edge designation may be

needed to ensure edges are appropriately scaled to ecological responses. Similarly, Uhrin and Holmquist (2003) showed decreases in faunal abundance at the edge of seagrass patches with lower crab and mollusk densities at smaller-scales, up to 5 meters away from seagrass scars, again supporting a somewhat larger definition of a seagrass edge. While there is need to validate this edge size across systems, these results suggest that edge designations for futures seagrass studies seagrass should be larger than two meters and overall designations need to be scaled to the response variables tested in order to accurately capture edge effects.

Differences in ecological responses between the post-disturbance study and the fine-scale edge effects study may have been driven in part by the nature of habitat disturbance and landscape context. The post-disturbance study occurred within one-year of the hurricane disturbance event and thus may not capture edge effects that are driven by longer-term processes. Specifically, it may take years for seagrass to fully respond to altered environmental conditions associated with habitat edges (Whitfield 2002), and thus measuring ecological responses within one year of the storm may not detect the full impact of habitat edges. Furthermore, seagrass edges in the post-disturbance were typically placed along unvegetated patches scoured out by the storm embedded with larger seagrass beds. Habitat edges for the fine-scale study, in contrast, existed along the edge of seagrass beds bordered by channels or larger expanses of unvegetated habitat. Thus these habitat edges may have persisted over longer timescales and being less sheltered, may be more sensitive to water flow. As organisms respond to environmental parameters associated with fragmentation at multiple spatial scales (Yeager et al. 2019),

landscape context may have mediated differences between the two studies herein. While I did not have data on fine-scale, temporal patterns in seagrass landscape configuration, such data should be useful in further explaining context-dependency in edge effects across systems.

Importantly, high among site variability together with limited sample sizes for some variables may have hindered the ability to detect edge effects in this study. Due to COVID-19 and the resulting lab closures in the spring and summer of 2020, sample processing was halted resulting in the loss of data points from the fine-scale edge study. Some variables have information from only two of the initial four sites limiting the ability to make generalizations across sites, although even with only two complete transects, seagrass shoot density, seagrass biomass, and epiphyte biomass was found to vary with distance to the edge. This suggests that more sampling may be needed to further detect edge effects and that lack of response in some ecological responses in this study should be interpreted with caution.

As habitat fragmentation is expected to increase with expanding urbanization and increased disturbance frequency, there is a greater need for detailed studies that inform scientists of the ecological effects of these changes. Seagrass habitats are among the most threatened marine ecosystems, with habitat fragmentation becoming more prevalent as losses accelerate (Duarte 2002, Duffy 2006). As the majority of marine edge effects studies have been done in seagrass beds, there is also a large pool of prior knowledge to compare edge effects across systems. (Carroll et al. 2009, Waycott et al. 2009, Bostrom et al. 2006, Bostrom et al. 2011). Even still, there is a general lack of consensus regarding

the overall effect of habitat edges on seagrass ecological structure function. My results suggest that edge effect may be particularly pronounced for seagrass itself, and that ecologically defined edges may be larger than the edge sizes assumed in many past studies. Time since disturbance and landscape context may help further refine future models on the importance of edge effects. Moreover, multi-trophic measurements and better empirical measurement of habitat edges may help resolve differential responses across studies. Such studies will be key in predicting the effects of anthropogenic habitat fragmentation on the ecological function of critical nearshore habitat like seagrass.

Response Variable Type	Sampling Tool	Set Time	Distance Set/Collected (cm)
Nekton community composition	Minnow Trap	4 h	0, 40, 80, 120, 160, 200, 300, 500, 700, 1000
Predation risk	Squid Pop	1 h	
Benthic macrofauna community	Seagrass Cores	Point measurement	0, 20, 40, 60, 80, 100, 120, 140, 160, 180, 200, 250, 300, 500, 700, 1000
Epiphyte biomass			
Seagrass biomass			
Seagrass morphometrics			
Salinity	SONDE	Point measurement	
Temperature			
Diel conductivity	Data Loggers	48 h	0, 50, 200, 500
Diel temperature			
Water flow	Plaster Cubes		

Table 1: Summary of ecological variables measured at varying distances for seagrass edge including sampling tool, set time, and transect distances from the edge at which each variable was measured.

lm(Total Seagrass Biomass ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	2.19	95.8	10.09	0.002	0.11
Site		243	0.25	0.19	0.27

Table 2: Linear model output for effect of bed position (edge vs. interior) and site on total seagrass biomass per core. SS = sum of squares.

lm(Aboveground Seagrass Biomass ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	0.52	4.28	2.73	0.10	0.04
Site		25.36	0.85	0.64	0.21

Table 3: Linear model output for effect of bed position (edge vs. interior) and site on aboveground biomass per core. SS = sum of squares.

lm(Belowground Seagrass Biomass ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	1.71	57.84	12.83	<0.01	0.12
Site		162.4	1.9	0.03	0.33

Table 4: Linear model output for effect of bed position (edge vs. interior) and site on belowground biomass per core. SS = sum of squares.

lm(Total Seagrass Shoots ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	1.35	35.8	2.01	0.16	0.02
Site		917	2.69	0.001	0.46

Table 5: Linear model output for effect of bed position (edge vs. interior) and site on total seagrass shoots per core.

lm(Epiphyte Biomass ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	1.92	70.4	3.61	0.06	0.02
Site		2653	7.16	<0.0001	0.68

Table 6: Linear model output for effect of bed position (edge vs. interior) and site on epiphyte biomass (ug/cm^2).

lm(Benthic Macrofaunal Abundance ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	0.36	1.32	0.04	0.85	<0.01
Site		599	0.88	0.61	0.43

Table 7: Linear model output for effect of bed position (edge vs. interior) and site on benthic macrofaunal abundance per core.

lm(Benthic Macrofaunal Species Richness ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	0.64	2.89	1.96	0.18	0.03
Site		80.4	3.03	0.02	0.73

Table 8: Linear model output for effect of bed position (edge vs. interior) and site on benthic macrofaunal species richness per core.

lm(Benthic Macrofaunal Species Evenness ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	<0.01	<0.0001	<0.01	0.95	<0.01
Site		0.28	0.68	0.76	0.51

Table 9: Linear model output for effect of bed position (edge vs. interior) and site on benthic macrofaunal species evenness per core.

lm(Nekton Abundance ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	5.94	1353	3.08	0.08	0.02
Site		4364	1.42	0.21	0.06

Table 10: Linear model output for effect of bed position (edge vs. interior) and site on nekton abundance.

lm(Nekton Species Evenness ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	-0.12	0.13	1.67	0.21	0.06
Site		0.35	0.67	0.90	<0.01

Table 11: Linear model output for effect of bed position (edge vs. interior) and site on nekton species evenness.

lm(Nekton Species Richness ~ Position +Site)	Estimate	SS	F- value	P-Value	η^2
Position	-1.12	10.1	6.32	0.02	0.15
Site		19	1.69	0.16	0.29

Table 12: Linear model output for effect of bed position (edge vs. interior) and site on nekton species richness.

lm(Temperature ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	0.04	45.7	<0.0001	<0.01
Site		121	983	<0.0001	0.99

Table 13: Linear model output for effect of distance from bed edge and site on temperature point measurements.

lm(Salinity ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.0001	<0.01	1.05	0.31	<0.0001
Site		27.0	3195	<0.0001	0.10

Table 14: Linear model output for effect of distance from bed edge and site on salinity point measurements.

lm(Mean Temperature ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	0.01	4.11	0.08	0.02
Site	.06	.79	25.8	<0.0001	0.95

Table 15: Linear model output for effect of distance from bed edge and site on data logger mean temperature.

lm(Temperature Range ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	0.01	0.79	0.41	<0.01
Site	-0.41	0.43	78.6	<0.0001	0.91

Table 16: Linear model output for effect of distance from bed edge and site on data logger temperature range.

lm(Mean Salinity ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	-<0.01	0.1	0.15	0.71	<0.01
Site	1.68	7.01	10.7	0.01	0.6

Table 17: Linear model output for effect of distance from bed edge and site on data logger mean salinity.

lm(Salinity Range ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	-<0.01	0.02	<0.01	0.96	<0.01
Site	-3.04	23.1	2.97	0.13	0.3

Table 18: Linear model output for effect of distance from bed edge and site on data logger salinity range.

lm(Plaster Loss ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	0.38	1.07	0.32	<0.01
Site	-9.75	470	1351	<0.0001	0.99

Table 19: Linear model output for effect of distance from bed edge and site on plaster cube loss.

lm(Total Seagrass Biomass ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	3.67	8.01	<0.01	0.21
Site	0.37	1.12	2.44	0.13	0.06

Table 20: Linear model output for effect of distance from bed edge and site on total seagrass biomass.

lm(Aboveground Seagrass Biomass ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	0.14	10.73	<0.01	0.19
Site	0.17	0.22	17.31	<0.01	0.31

Table 21: Linear model output for effect of distance from bed edge and site on aboveground seagrass biomass.

lm(Belowground Seagrass Biomass ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	0.001	2.38	6.64	0.01	0.18
Site	0.21	0.34	0.96	0.34	0.03

Table 22: Linear model output for effect of distance from bed edge and site on belowground seagrass biomass.

lm(Epiphyte biomass ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	125.5	4.57	0.04	0.12
Site	3.67	107	3.92	0.06	0.1

Table 23: Linear model output for effect of distance from bed edge and site on epiphyte biomass.

lm(Total Seagrass Shoots ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.01	11.9	10.7	0.002	0.27
Site	0.19	0.28	0.25	0.62	<0.01

Table 24: Linear model output for effect of distance from bed edge and site on total seagrass shoots.

lm(Benthic Macrofaunal Abundance ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	-<0.01	0.09	0.06	0.81	<0.01
Site	-0.69	3.78	2.68	0.11	0.08

Table 25: Linear model output for effect of distance from bed edge and site on benthic macrofaunal abundance.

lm(Benthic Macrofaunal Species Richness ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	0.52	0.19	0.41	0.52	0.01
Site		0.83	0.60	0.62	0.05

Table 26: Linear model output for effect of distance from bed edge and site on benthic macrofaunal species richness.

lm(Nekton Abundance ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	-<0.01	0.04	<0.01	0.962	<0.0001
Site		408	6.76	<0.01	0.04

Table 27: Linear model output for effect of distance from bed edge and site on nekton abundance.

lm(Nekton Species Richness ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	-<0.01	0.11	0.29	0.59	<0.01
Site		11.8	<0.0001	<0.0001	0.46

Table 28: Linear model output for effect of distance from bed edge and site on nekton species richness.

glm(Predation Rate ~ Distance +Site)	Estimate	SS	F- value	P-Value	η^2
Distance	<0.0001	<0.01	<0.01	0.93	<0.01
Site	-0.8	4.72	14.9	<0.0001	0.57

Table 29: Linear binomial regression model output for effect of distance from bed edge and site on squid pop predation rates.

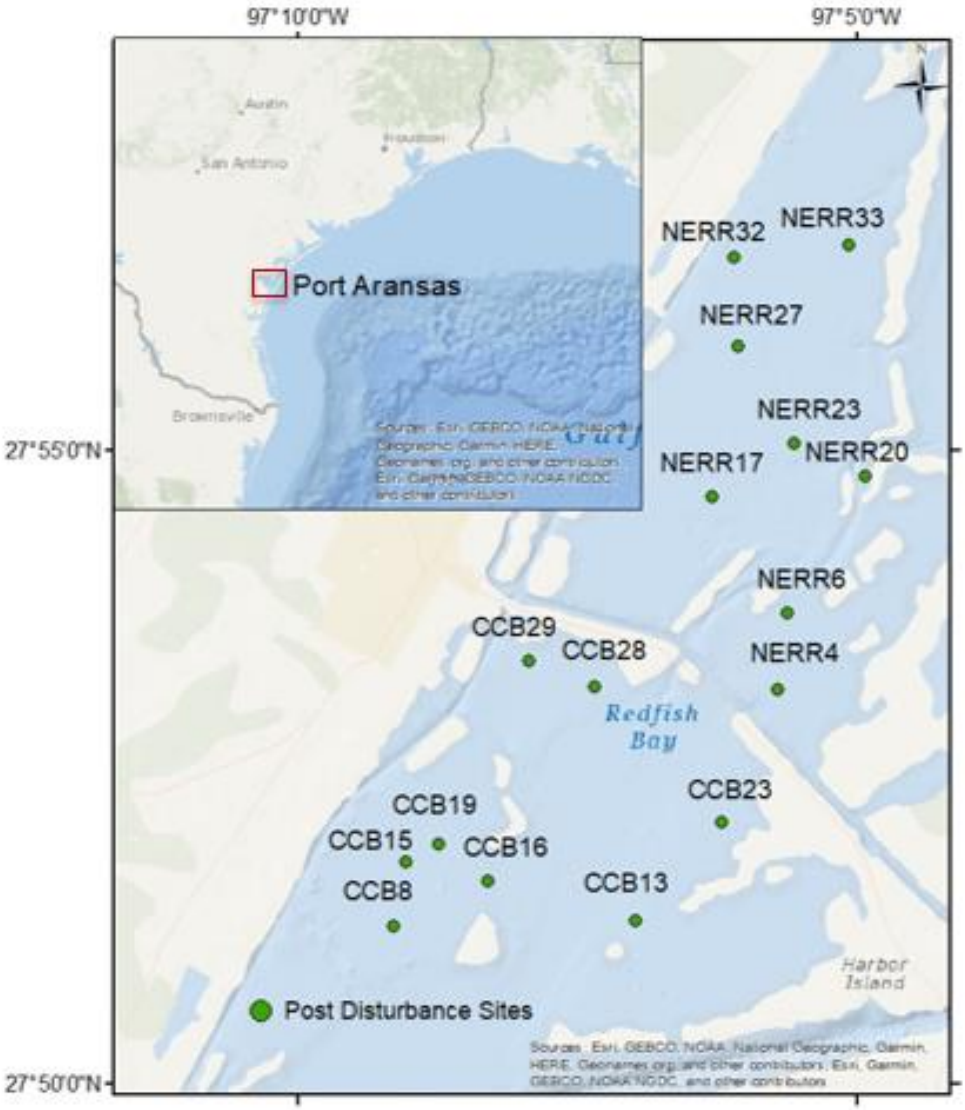

Figure 1: Post-disturbance study sites sampled in Corpus Christi Bay, Texas, USA.

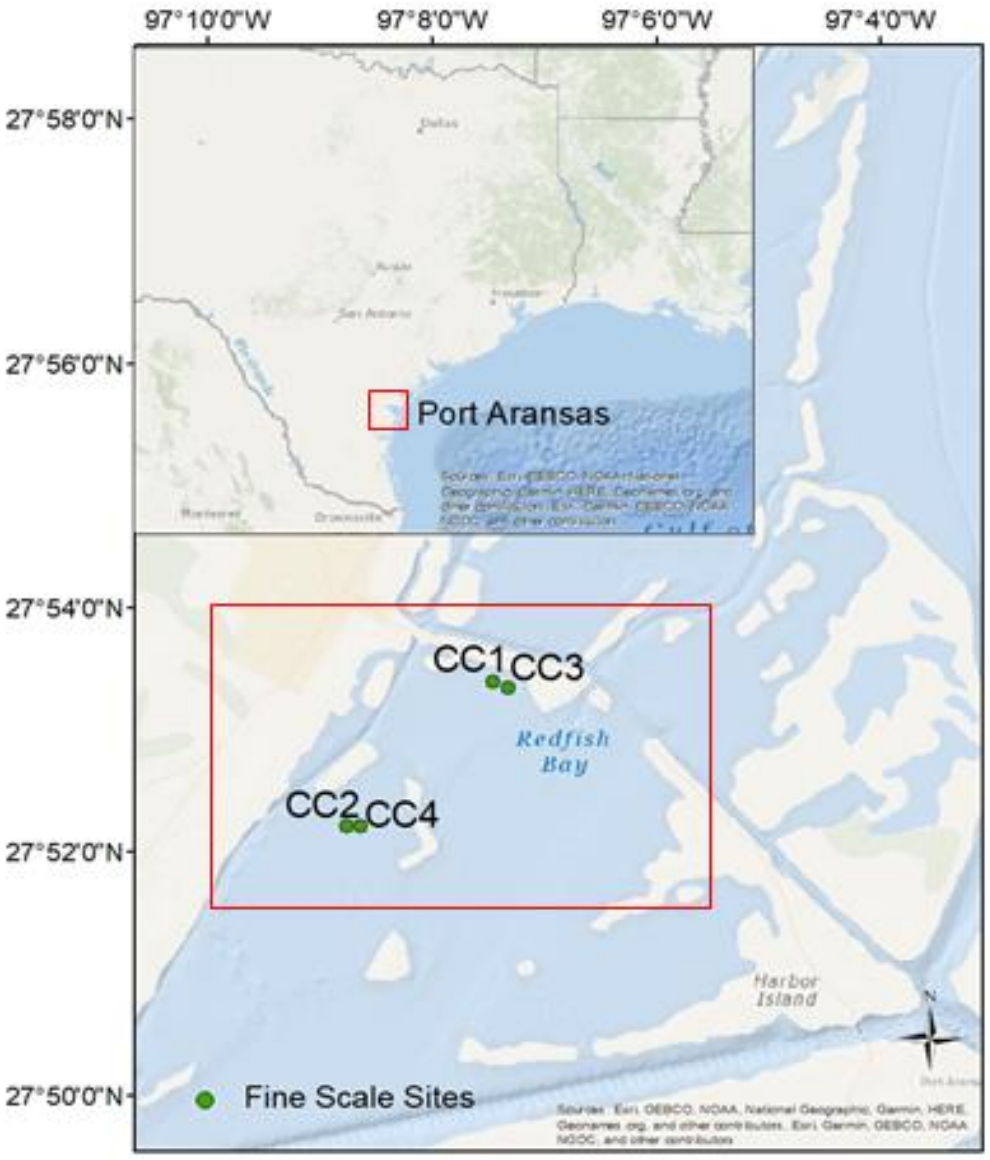

Figure 2: Fine-scale edge study sites sampled in Corpus Christi Bay, Texas, USA.

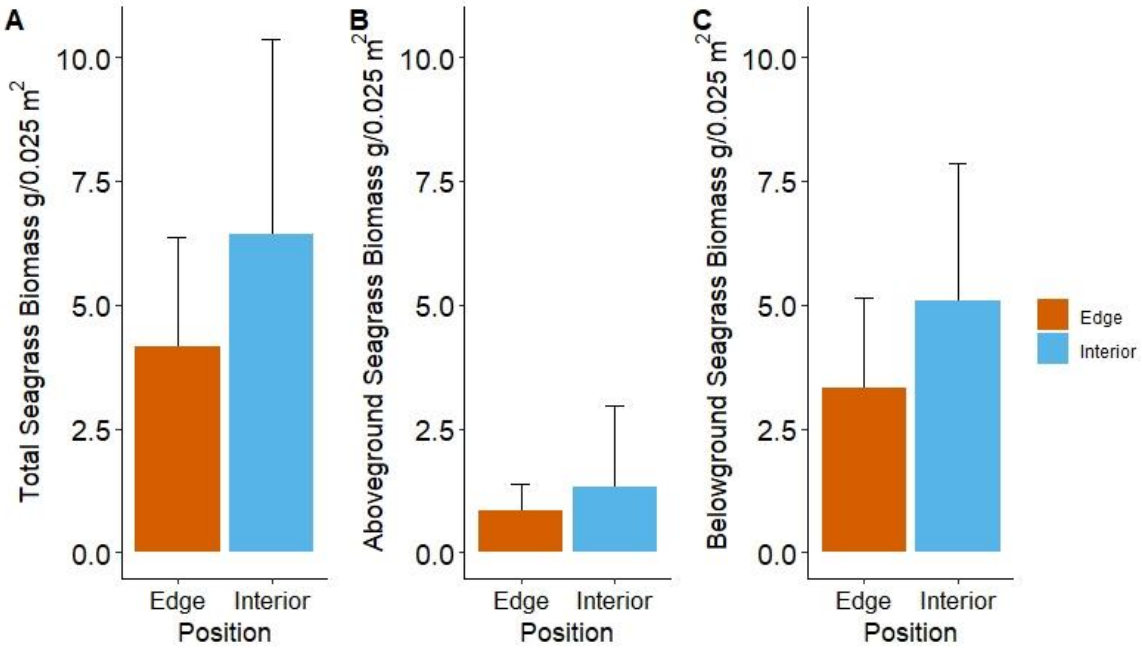

Figure 3: Total Seagrass Biomass (A), Aboveground Seagrass Biomass (B), Belowground Seagrass Biomass (C) per core (g/0.025 m^2) compared between edge and interior position (mean + SD).

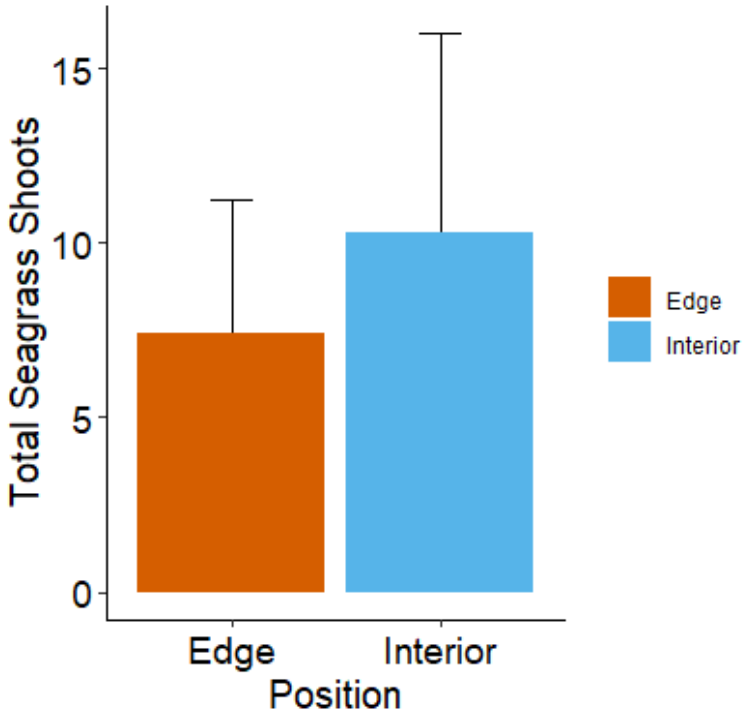

Figure 4: Total seagrass shoots per core (shoots/0.025 m^2) compared between edge and interior position (mean + SD).

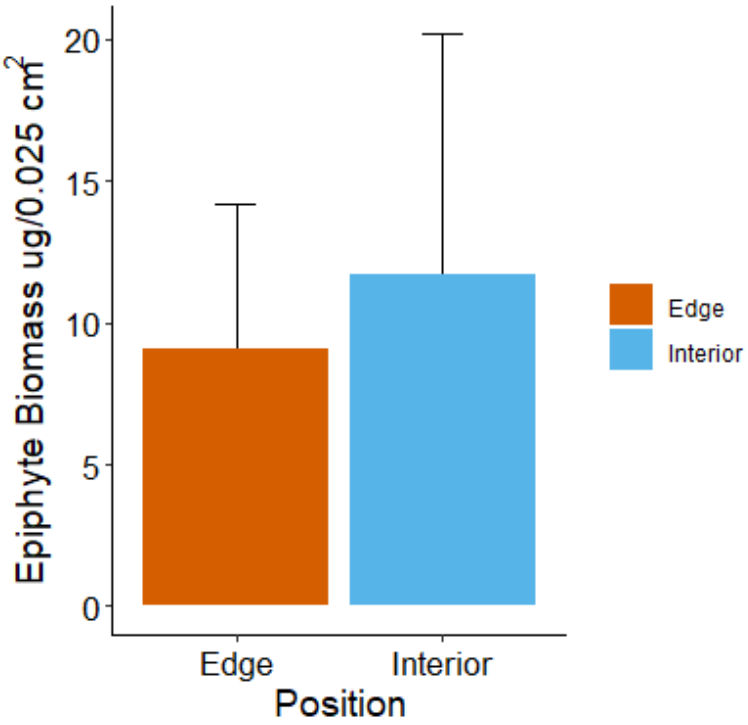

Figure 5: Epiphyte biomass scaled by blade area per core (ug/cm^2) compared between edge and interior position (mean + SD).

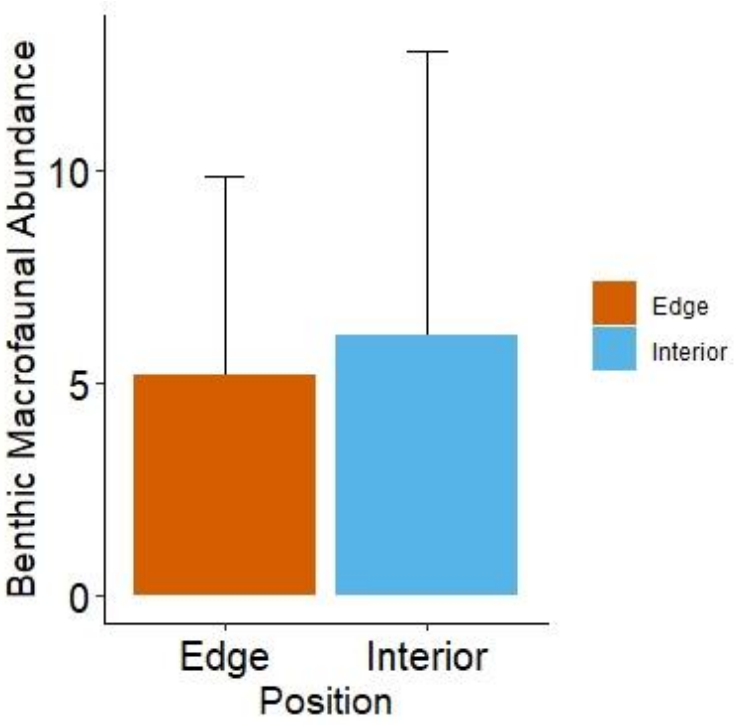

Figure 6: Benthic macrofaunal abundance (organisms/0.025 m^2) compared between edge and interior position (mean + SD).

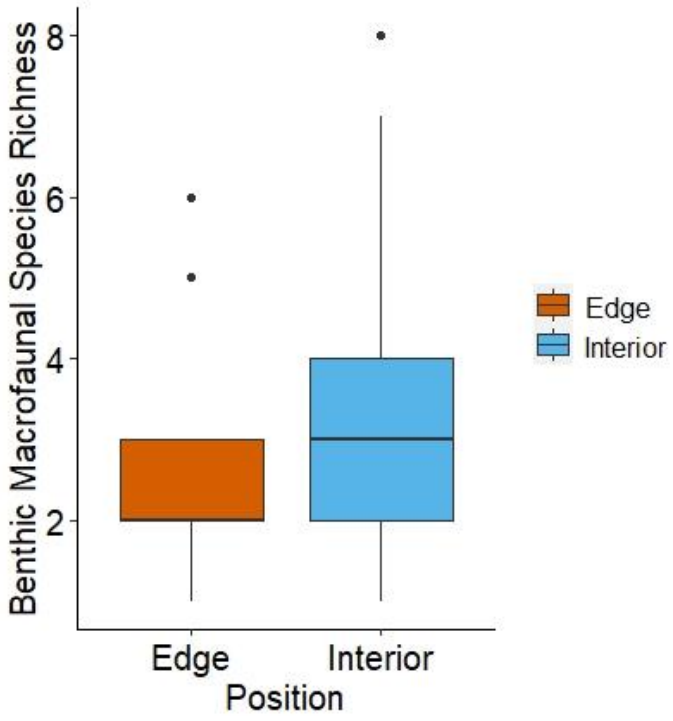

Figure 7: Benthic macrofaunal species richness (number of species/0.025 m^2) compared between edge and interior position.

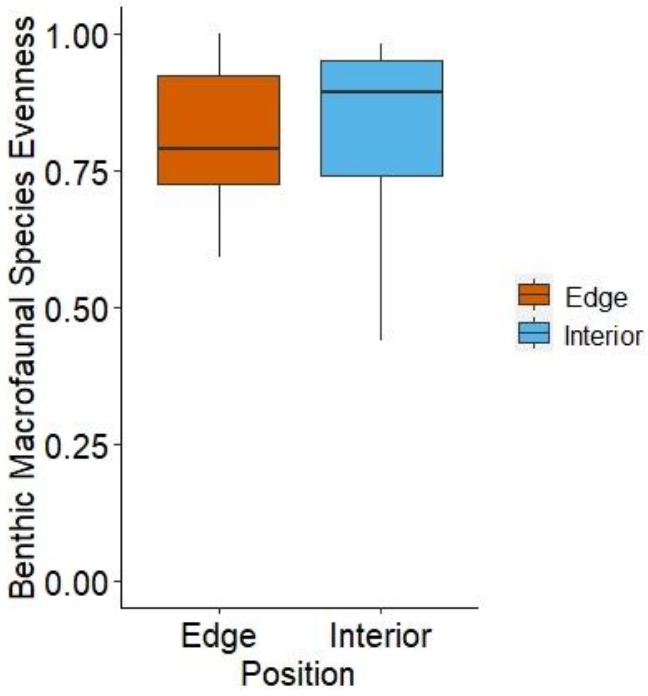

Figure 8: Benthic macrofaunal species evenness (calculated evenness/0.025 m^2) compared between edge and interior position.

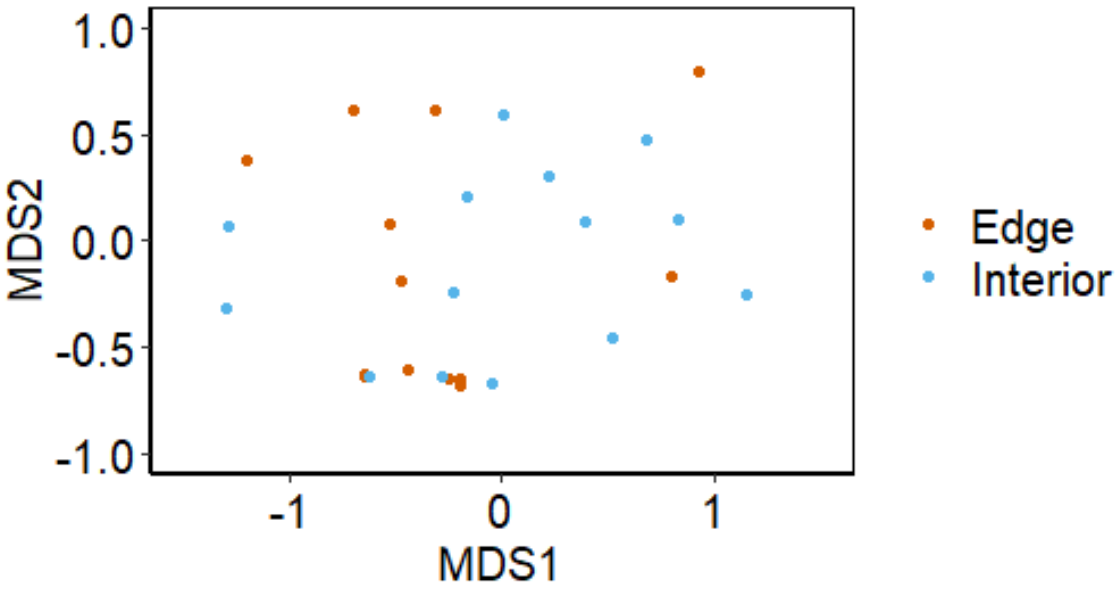

Figure 9: Benthic macrofaunal community composition compared between edge and interior position (R^2:0.03, P-value:0.25. SS:0.382, Stress= 0.13).

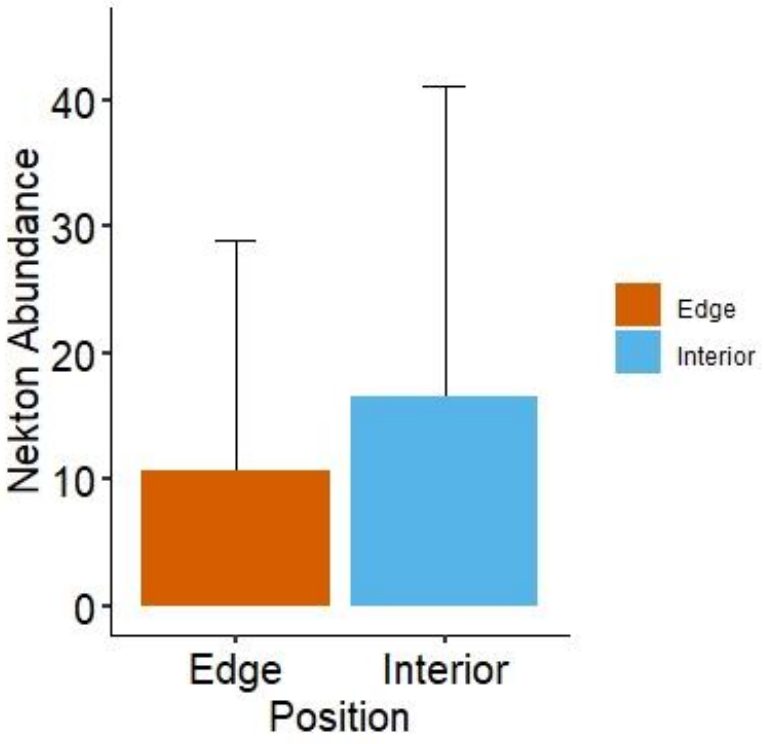

Figure 10: Nekton abundance of nekton compared between edge and interior position (mean + SD).

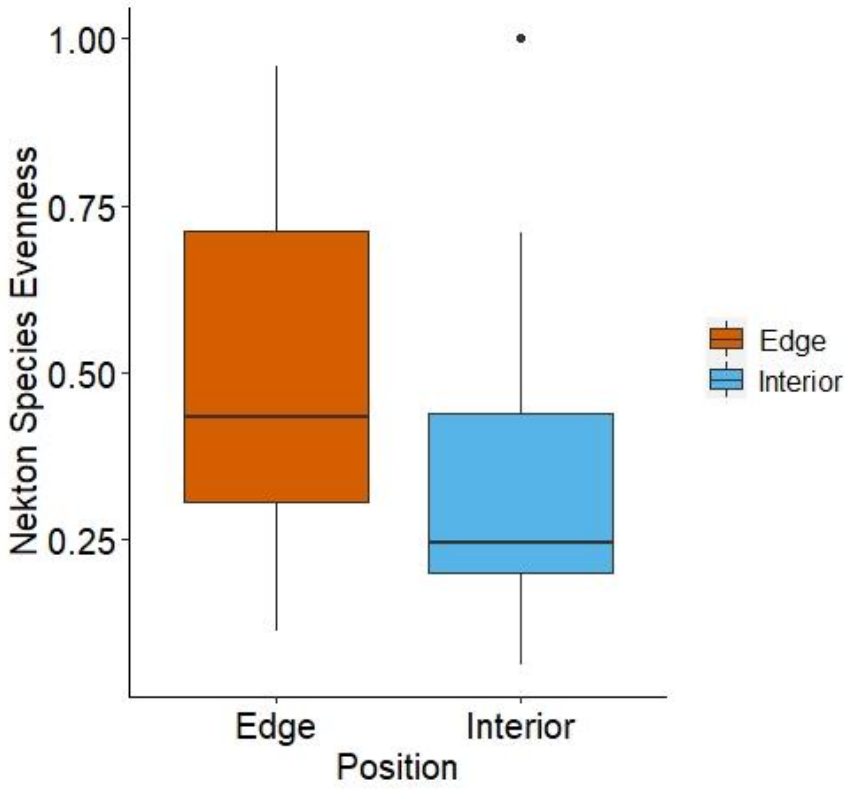

Figure 11: Nekton species evenness compared between edge and interior position.

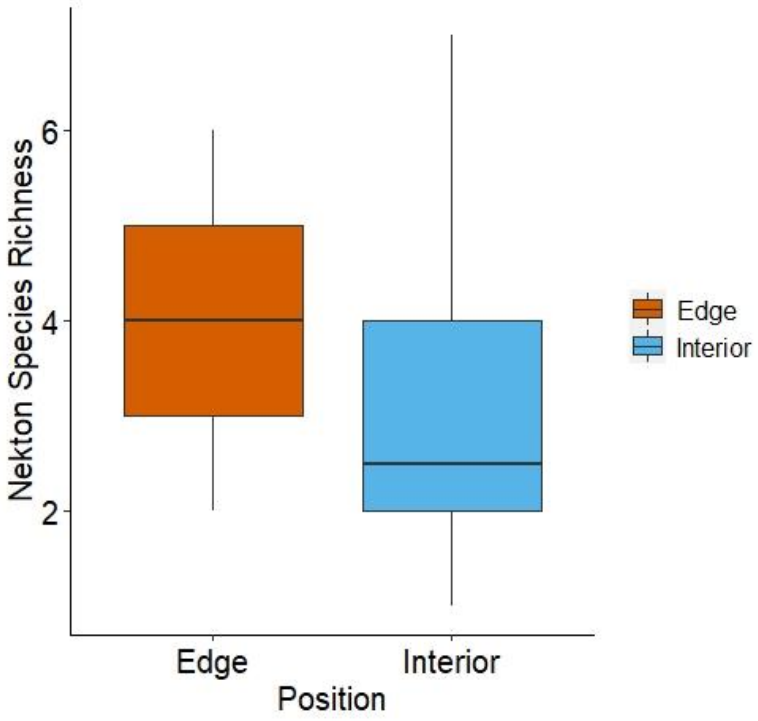

Figure 12: Nekton species richness compared between edge and interior position.

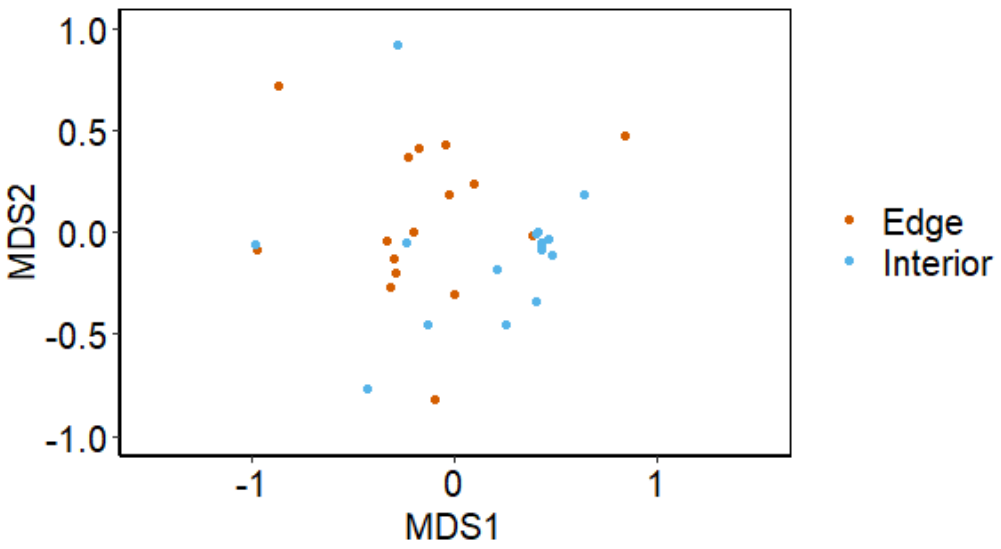

Figure 13: Nekton community composition compared between edge and interior position (R-squared:0.07, p-value:0.03, SS = 0.292, Stress= 0.15).

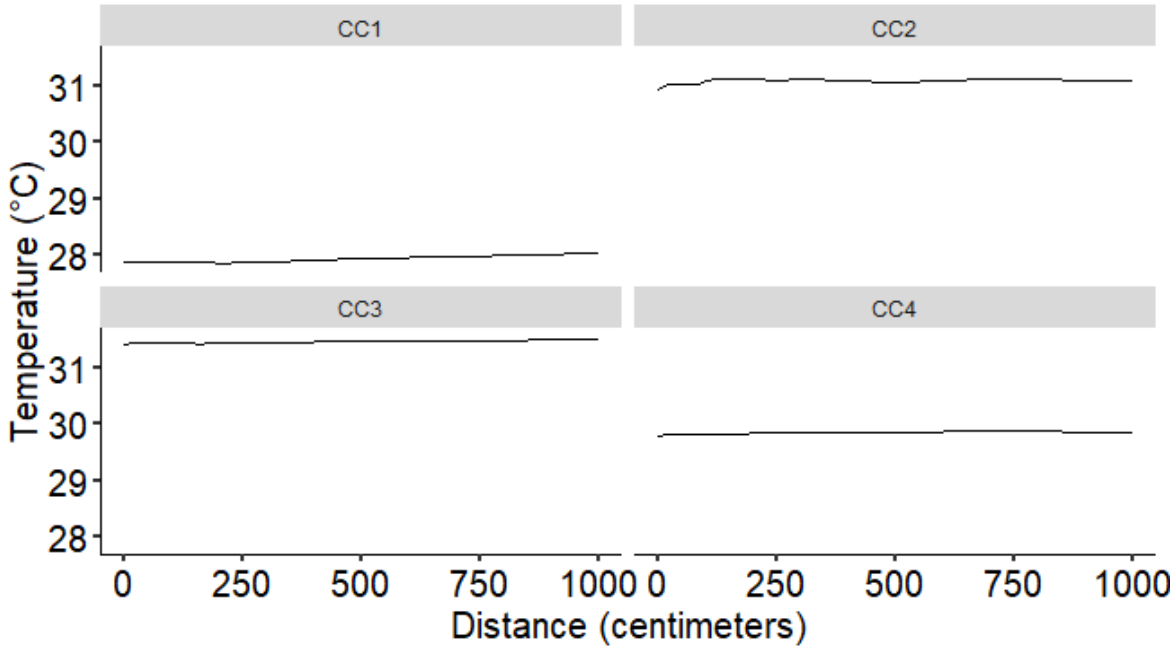

Figure 14: Temperature (°C) from point YSI measurements plotted against distance from seagrass edge towards bed interior.

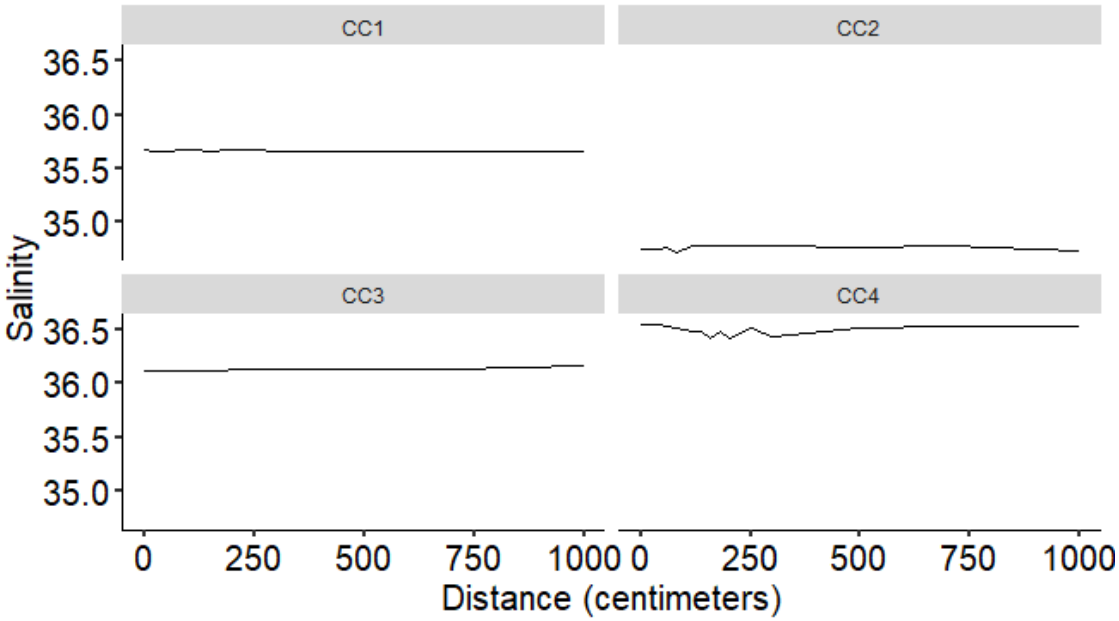

Figure 15: Salinity from point YSI measurements plotted against distance from seagrass edge towards bed interior.

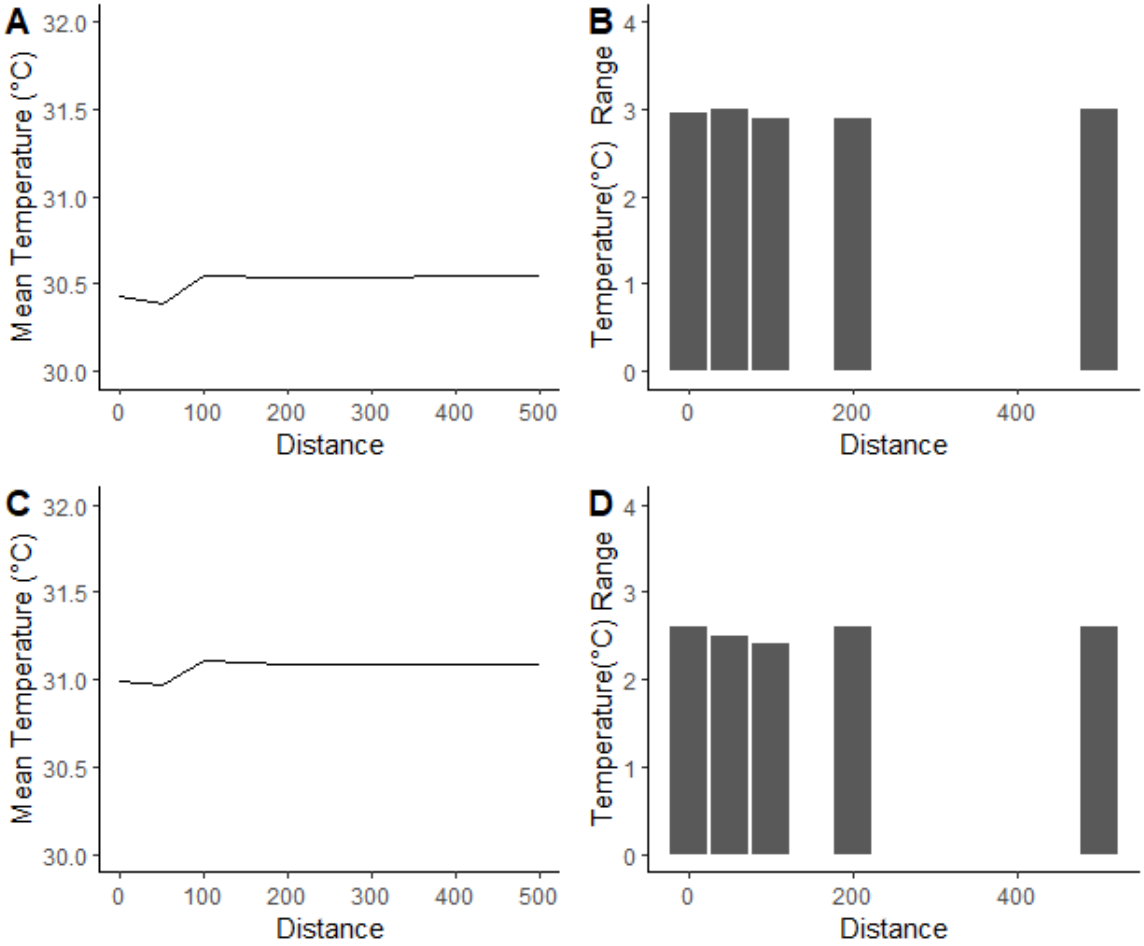

Figure 16: Data Logger temperature(°C) over 48 hours plotted against distance from seagrass edge towards bed interior. Plots A and B are transect CC1 and C, D are transect CC3.

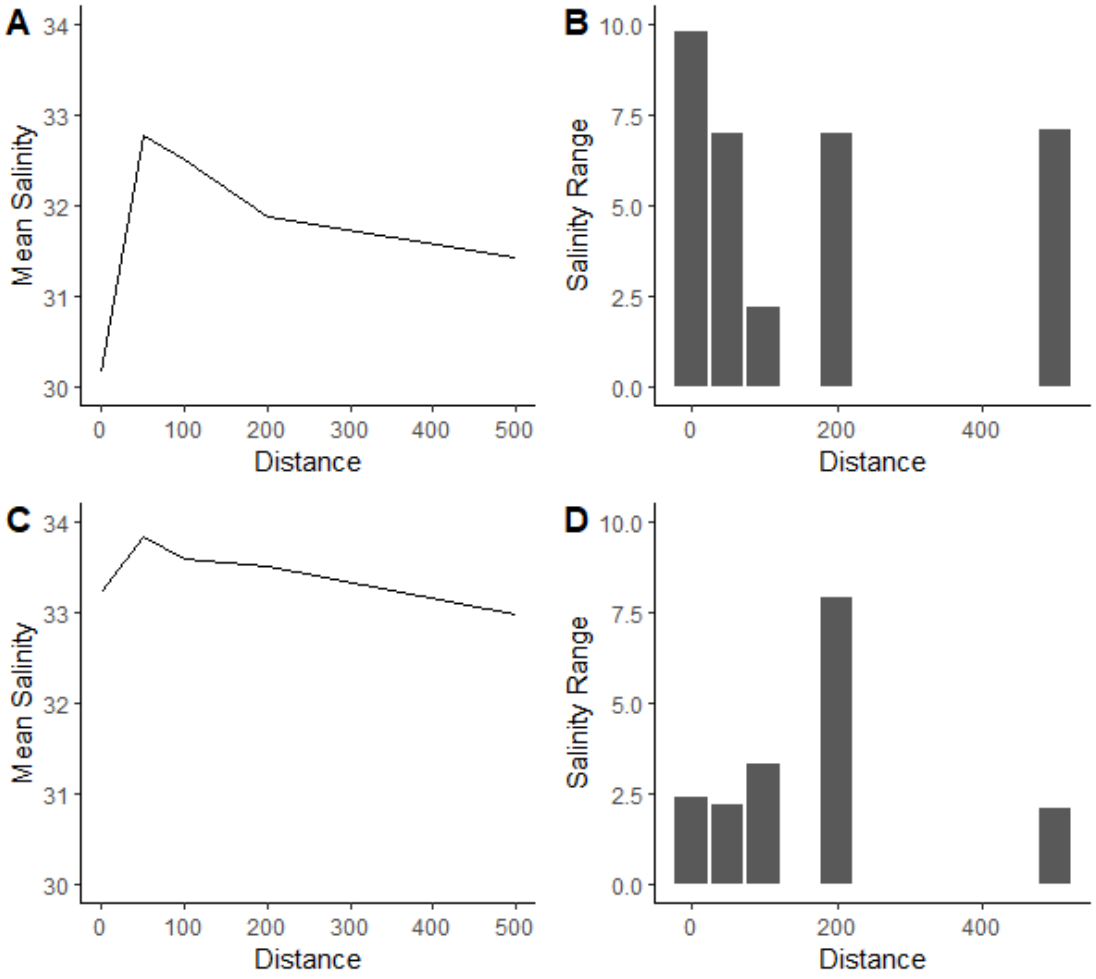

Figure 17: Data Logger temperature over 48 hours plotted against distance from seagrass edge towards bed interior. Plots A and B are transect CC1 and C, D are transect CC3.

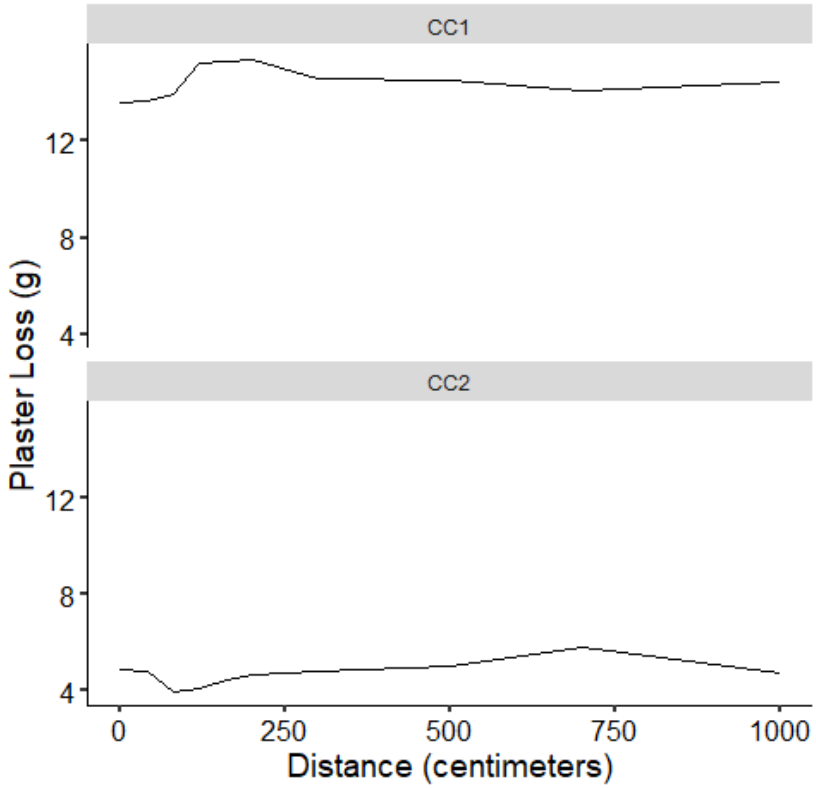

Figure 18: Plaster loss (g) as a proxy for flow plotted against distance from seagrass edge towards bed interior.

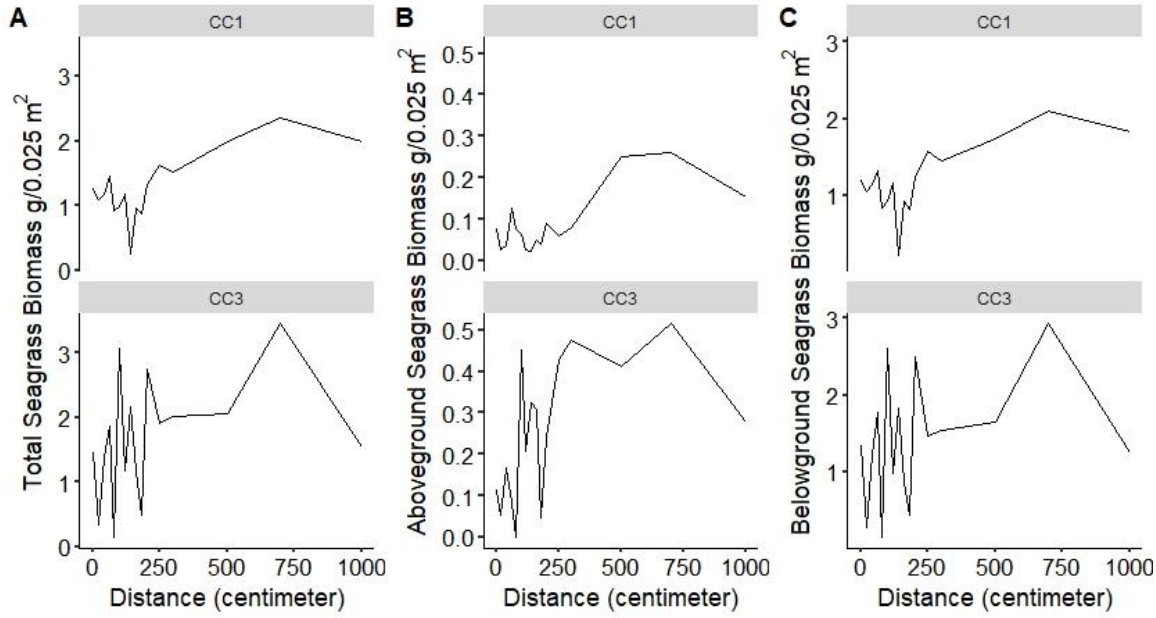

Figure 19: Total Seagrass Biomass (A), Aboveground Seagrass Biomass (B), Belowground Seagrass Biomass (C) per core (g/0.025 m^2) plotted against distance from seagrass edge towards bed interior.

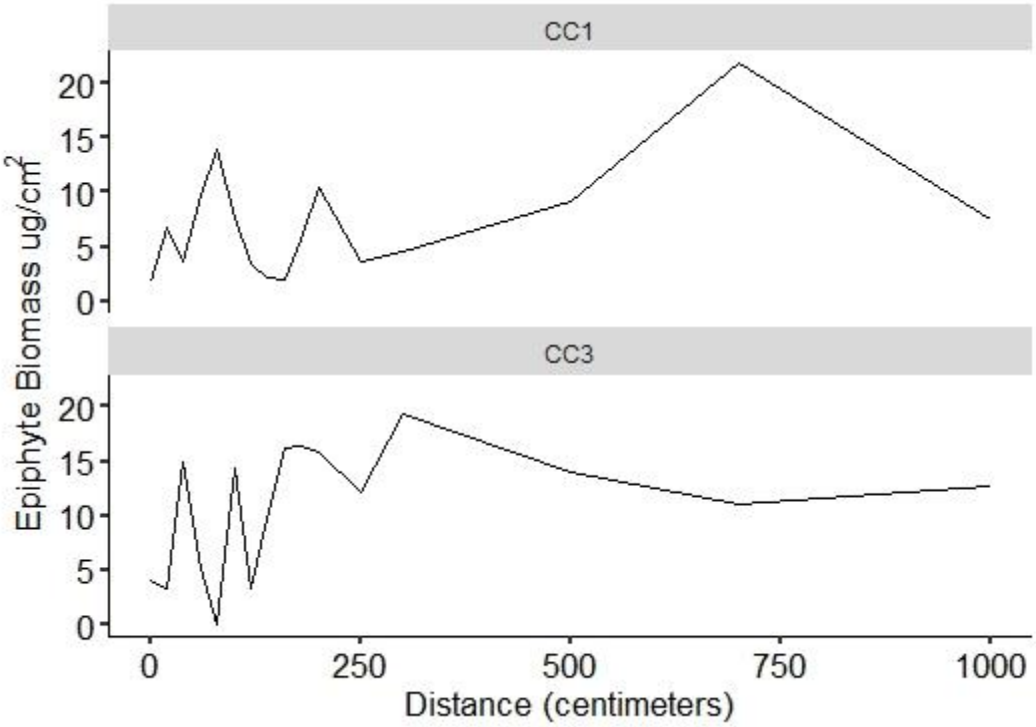

Figure 20: Epiphyte biomass (ug/cm^2) adjusted by shoot area plotted against distance from seagrass edge towards bed interior.

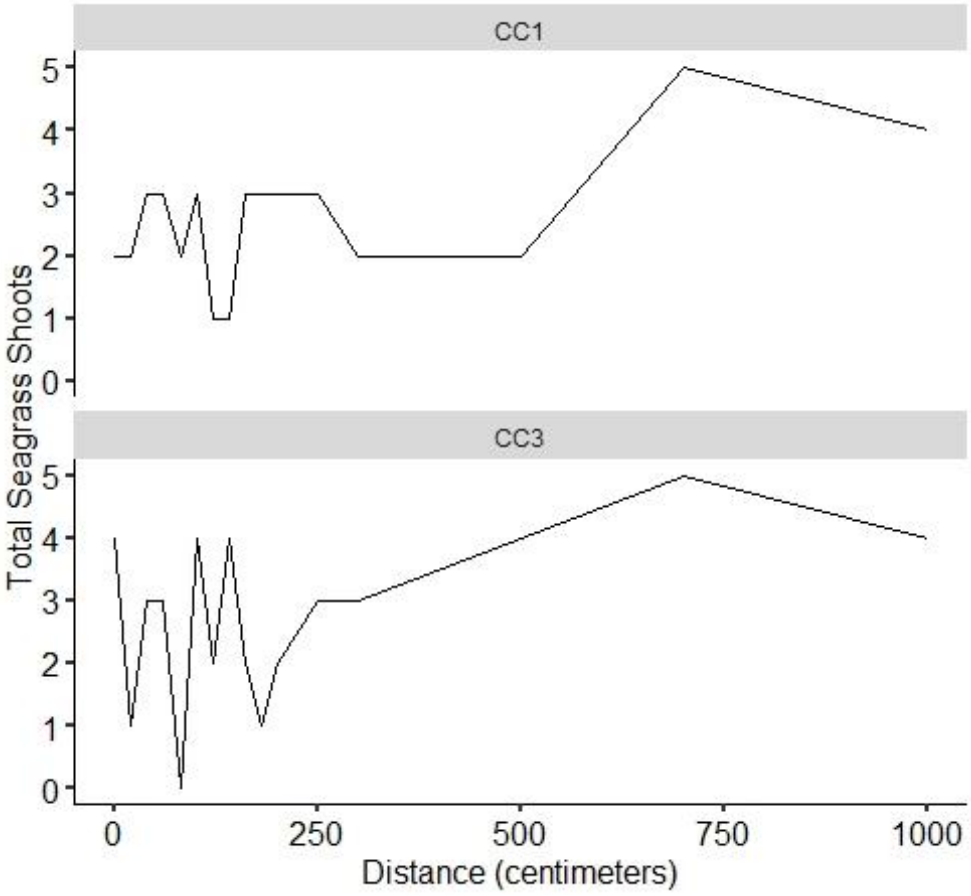

Figure 21: Total seagrass shoots (shoots/0.025 m^2) plotted against distance from seagrass edge towards bed interior.

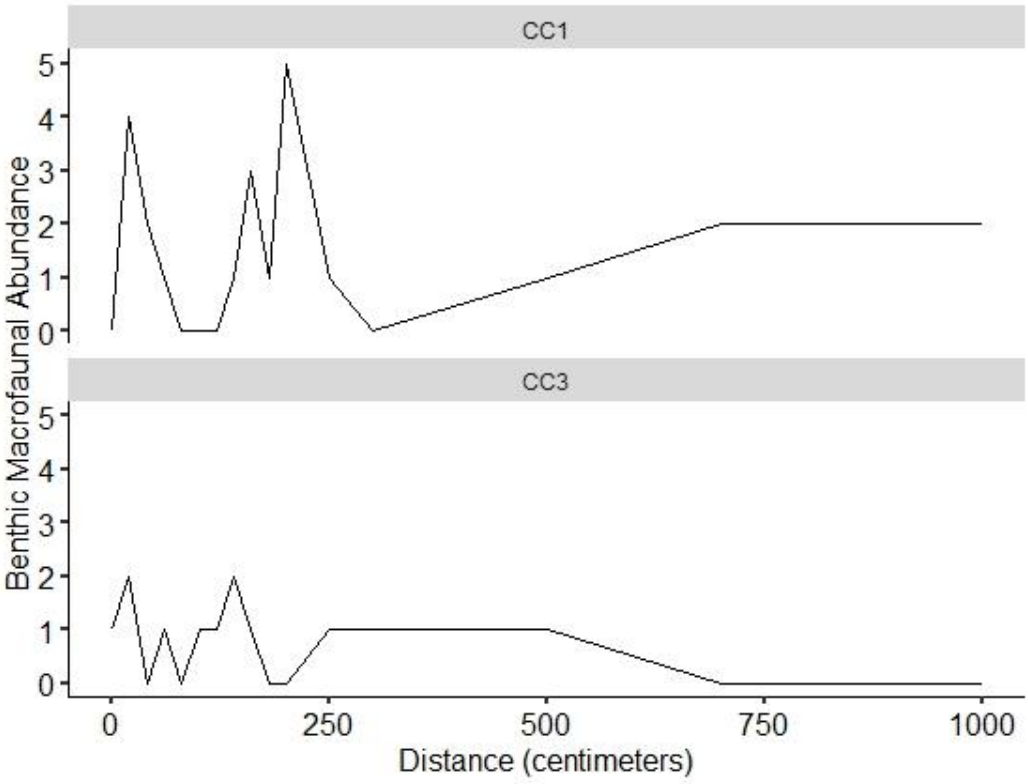

Figure 22: Benthic macrofaunal abundance plotted against distance from seagrass edge towards bed interior.

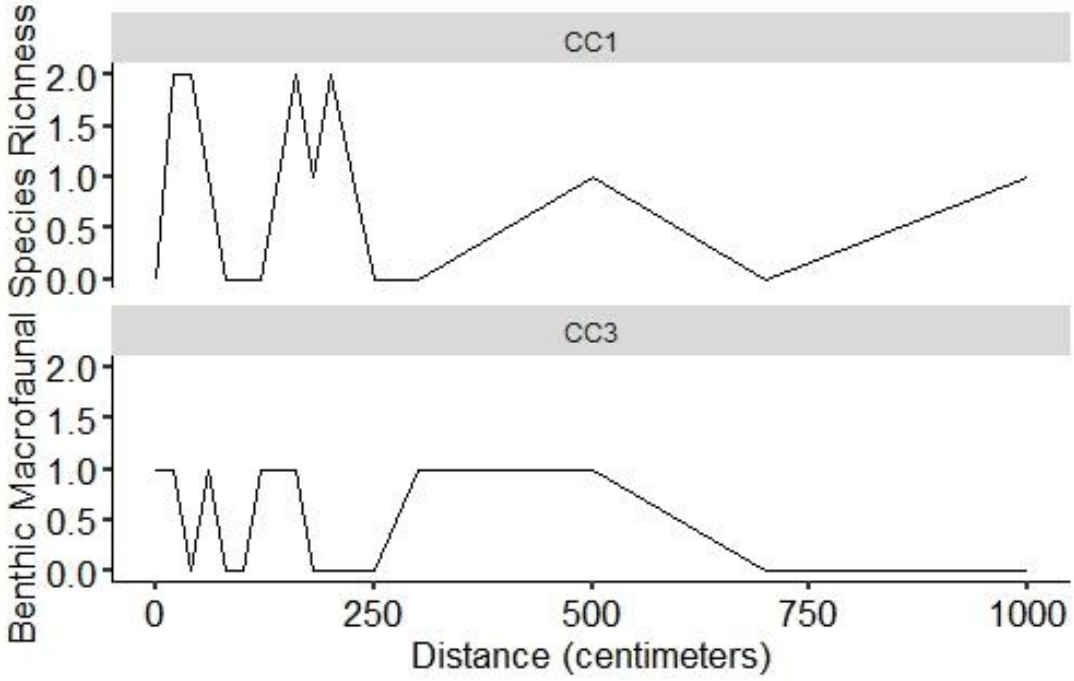

Figure 23: Benthic macrofaunal species richness plotted against distance from seagrass edge towards bed interior.

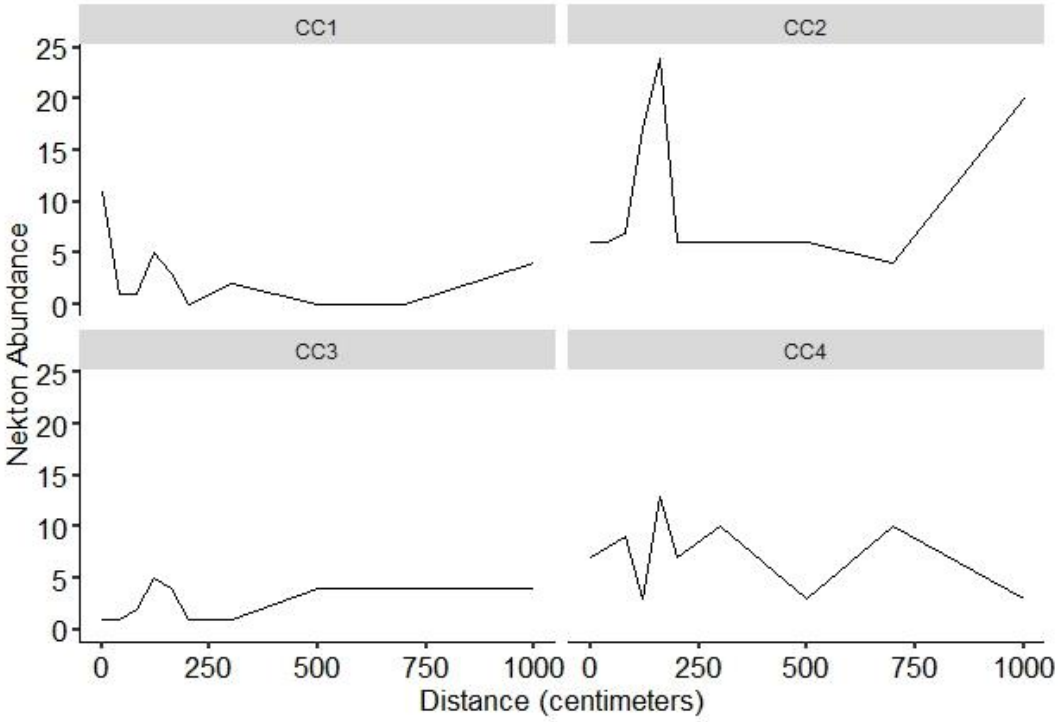

Figure 24: Nekton abundance plotted against distance from seagrass edge towards bed interior.

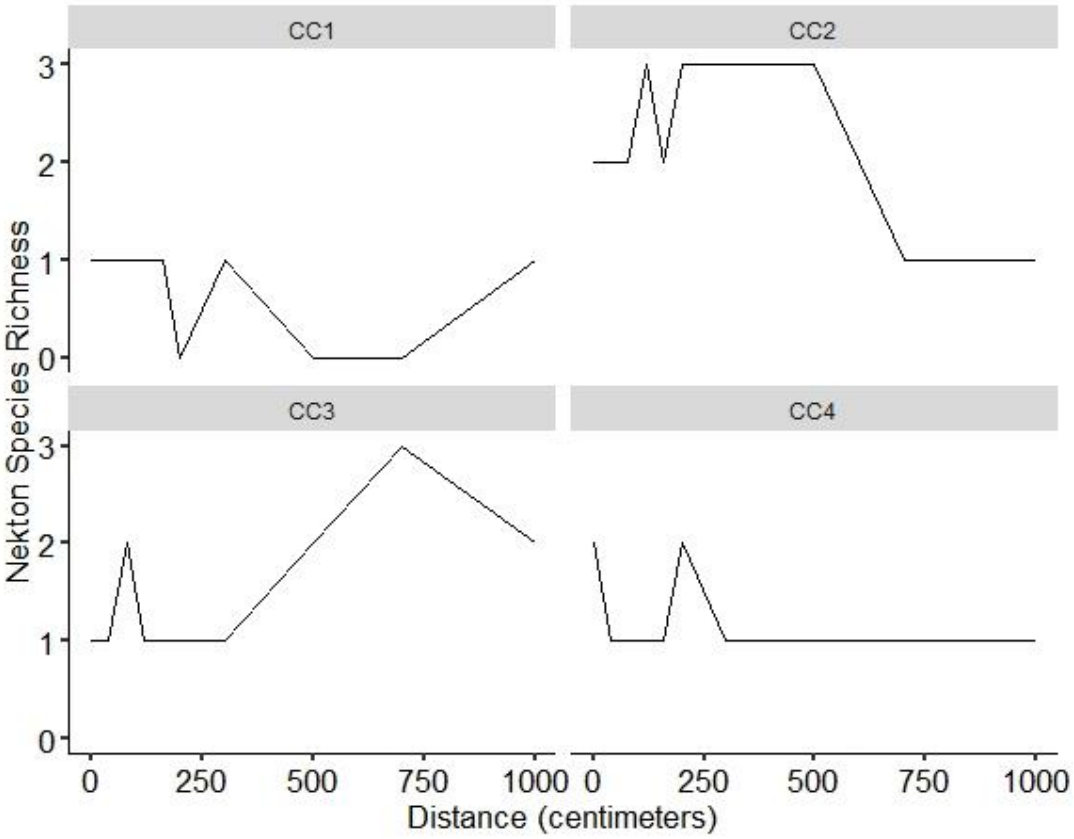

Figure 25: Nekton species richness plotted against distance from seagrass edge towards bed interior.

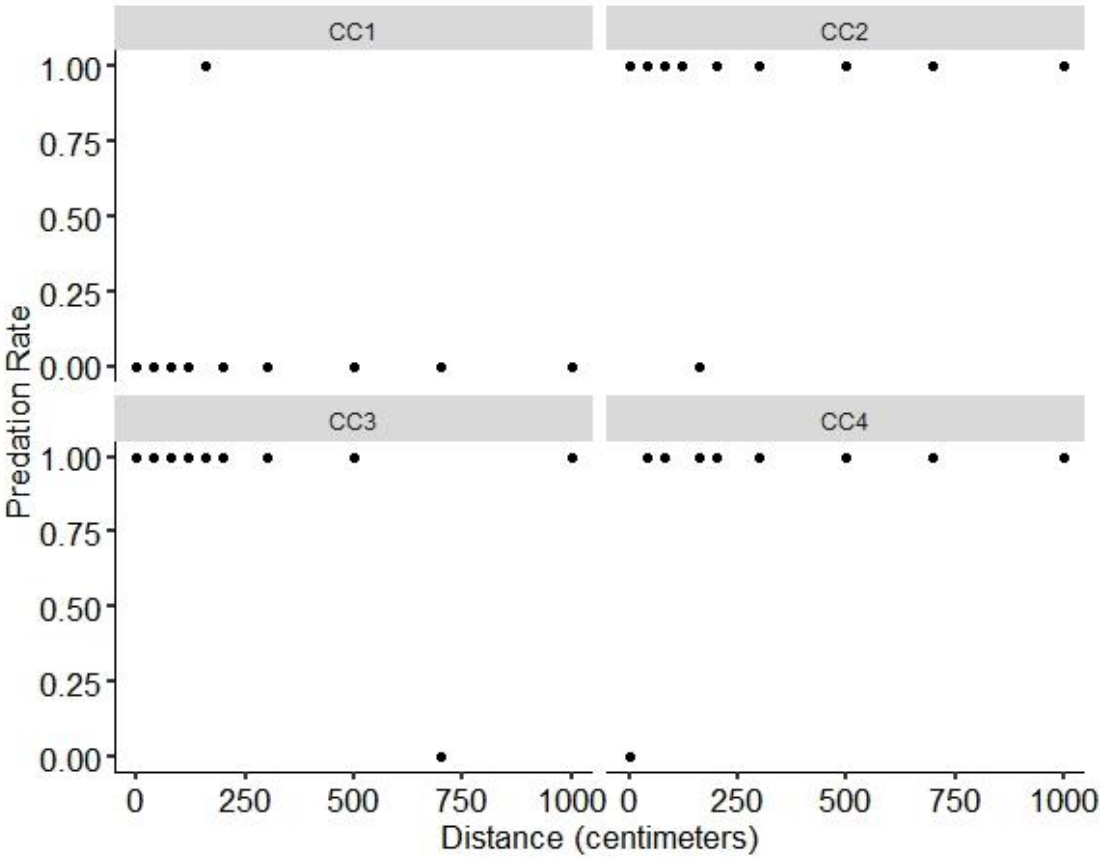

Figure 26: Predation rates from squid pop surveys (Predation = 1) plotted against distance from seagrass edge towards bed interior.

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